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On the biology of Ernstkeller's cave gecko, *Gekko ernstkelleri* Rösler, Siler, Brown, Demegillo et Gaulke, 2006 (Squamata: Gekkonidae), with emphasis on reproductive biology

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Abstract: *Gekko ernstkelleri* Rösler, Siler, Brown, Demegillo et Gaulke, 2006 is a medium sized member of the genus *Gekko* Laurenti, 1768, endemic to the central Philippine Island of Panay. This rupicolous species inhabits limestone outcrops, especially entrance areas of limestone caves. It is mainly nocturnal. Four pairs of *G. ernstkelleri* were kept in husbandry for eight years, and their species-specific behaviour and breeding biology recorded. No agonistic behaviour was observed among couples living permanently together, while males display territorial induced aggressive behaviour towards each other. *G. ernstkelleri* is oviparous. Egg clutches contain one or two hard-shelled eggs. Fertile eggs are attached to inorganic substrates such as glass or plastic tubes. In captivity, juveniles hatched after 64–179 days. Snout-vent length (SVL) of hatchlings is 29.5–39.5 mm, tail length (TaL) 31.0–47.0 mm, and weight 0.6382–1.1632 g. The relative clutch weight varies between 9.87% and 21.08%.

Key words: Sauria, *Gekko ernstkelleri*, description, distribution, ecology, behaviour, reproduction.

Introduction

With a land area of around 12 000 km^2, Panay is the sixth-largest island of the Philippine Archipelago. The herpetology of Panay is fairly well explored (e.g. Ferner *et al*. 2001; Gaulke 2011).

Thirteen gecko species (family Gekkonidae Gray, 1825) are recorded from the island. Seven of them are endemic to the Philippines, but only *Gekko ernstkelleri* is endemic to Panay (Rösler *et al*. 2006). The present chapter deals with behavioural observations made during eight years of husbandry of this species, as well as with observations in nature.

Material and methods

Occasional field observations on *Gekko ernstkelleri* are recorded by one of the authors (M. Gaulke) since 2004. Observations and investigations on four pairs of *G. ernstkelleri* kept in husbandry by the first author (HR) are recorded since 2013. Both data sets are compared and / or supplemented, to obtain a profound knowledge on the biology of *G. ernstkelleri*, with emphasis on reproductive biology.

The geckos were kept in four equivalent glass-terraria with similar equipment. Air temperature and relative humidity were recorded in a 24 hour cycle for one year with a hygrothermograph. Climatic terraria conditions were not equivalent to conditions in nature, especially winter temperatures inside the terraria were significantly lower than on Panay. The geckos were fed with different insects and insect larvae, vegetarian food was not ingested.

Morphometric parameters (size of living adults and juveniles, egg-length and egg-width) were measured with a digital caliper, thickness of eggshells with a micrometer. The weight of eggs, eggshells, and juveniles was taken with a pharmaceutical micro scale, adult weight with a laboratory scale.

The reproductive effort (= relative clutch mass, RCM) was determined by using formulas from Pianka & Pianka (1976) and Hielen (1993), egg-volume with the formula $4/3\pi ab^2$.

Abbreviations used in the text:

SVL – snout-vent length;
TaL – tail length;
BW – body weight;
EL – egg length;
EW – egg width.

Results

Short description and systematics

With a total length of around 200 mm (max. SVL 92 mm), *G. ernstkelleri* Rösler, Siler, Brown, Demegillo et Gaulke, 2006 is a medium-sized member of the genus *Gekko*. SVL of mature males 82–92 mm (N = 8), of mature females 78–85 mm (N = 10), TaL/SVL 1.18–1.36 (data recorded from free ranging individuals on Panay, Gaulke 2011).

Gekko ernstkelleri is specific due to the following features: 11–15 dorsal tubercle rows; 14–18 subdigital scansors on first, and 16–19 on fourth finger; 15–17 subdigital scansors on first, and 17–19 on fourth toe; dorsal tail tubercles only up to fifth caudal whorl; subcaudals enlarged. Males can be determined by enlarged cloacal tubercles and 36 – 42 preanofemoral pores, which are absent in females (Rösler *et al*. 2006).

The life coloration of *G. ernstkelleri* is somewhat variable. The dorsal side is olive to brown-olive, with distinctive whitish and dark-brown spots. The different-sized whitish spots are arranged in irregular transverse rows across the dorsum, being more prominent on head and nuchal region, and fading caudad in intensity and size. Paired dark-brown spots are present on the vertebral region. While they are arranged in transverse rows posteriorly, they sometimes merge in the nuchal region and on the head into darkish skin patches. The dorsal side of the tail is dark and light banded, with the light bands being about half as wide as the dark bands. Around the posterior part of the tail, the light bands can build confluent rings. The dark interspaces have blackish-brown margins, and are mottled brown in between. Especially in males they can be blackish-brown throughout. Gular region and venter are light yellowish to light greyish-brown, with fine brown dotting. The ventral side of the tail is light yellowish-brownish with large brown blotches, which become denser towards the tail-tip (Fig. 1). Males are occasionally more distinctly colored than females (Fig. 2).

Within the genus *Gekko* the species *G. ernstkelleri* belongs to the *Gekko monarchus* group (Rösler *et al*. 2011).

Wood *et al*. (2020) published a phylogeny and systematic concept of the *Gekko* clade, and suggested an arrangement in seven subgenera. For the Philippine species-complex they introduced the subgenus *Archipelagekko* Wood, Guoa, Travers, Su, Olson, Bauer, Grismer, Siler, Moyle, Andersen et Brown, 2020. This phylogenetic lineage contains, with exception of *G. gecko*, all other Philippine species of the genus *Gekko* (*G. athymus* Brown et Alcala, 1962, *G. carusadensis* Linkem, Siler, Diesmos, Sy et Brown, 2010, *G. coi* Brown, Siler, Oliveros, Diesmos et Alcala, 2011, *G. crombota* Brown, Oliveros, Siler et Diesmos, 2008, *G. ernstkelleri* Rösler, Siler, Brown, Demegillo et Gaulke, 2006, *G. gigante* Brown et Alcala, 1978, *G. mindorensis* Taylor, 1919, *G. monarchus* [Schlegel, 1836], *G. palawanensis* Taylor, 1925, *G. porosus* Taylor, 1922, *G. romblon* Brown et Alcala, 1978, *G. rossi* Brown, Oliveros, Siler et Diesmos, 2009), as well as *G. kikuchii* Oshima, 1912, which is distributed up to Lanyu Island, Taiwan. All species of the subgenus *Archipelagekko* resemble each other widely regarding their phenotype (head-, body- and tail-shape; SVL < TaL; similar coloration and dorsal color pattern) (Brown & Alcala 1962; 1978; Brown *et al*. 2008; 2009; 2011; Linkem *et al*. 2010; Rösler *et al*. 2011).

Distribution

To present knowledge, *G. ernstkelleri* is endemic to Panay Island, and on Panay only known from different locations of the Northwest Panay Peninsula, from the Provinces of Antique and Aklan. It occurs from sea level up to around 300 m asl (Gaulke 2011).

Ecology

Gekko ernstkelleri is an inhabitant of limestone karst habitats. Most specimens were sighted in the entrance areas of limestone caves within or close to secondary or primary lowland limestone forests (Fig. 3). Tunnel-like caves with wide entrance areas on both sides are occupied throughout (Fig. 4). A few individuals were sighted on trees surrounding cave entrances, and on deeply corroded rocky limestone outcrops close to the coastline.

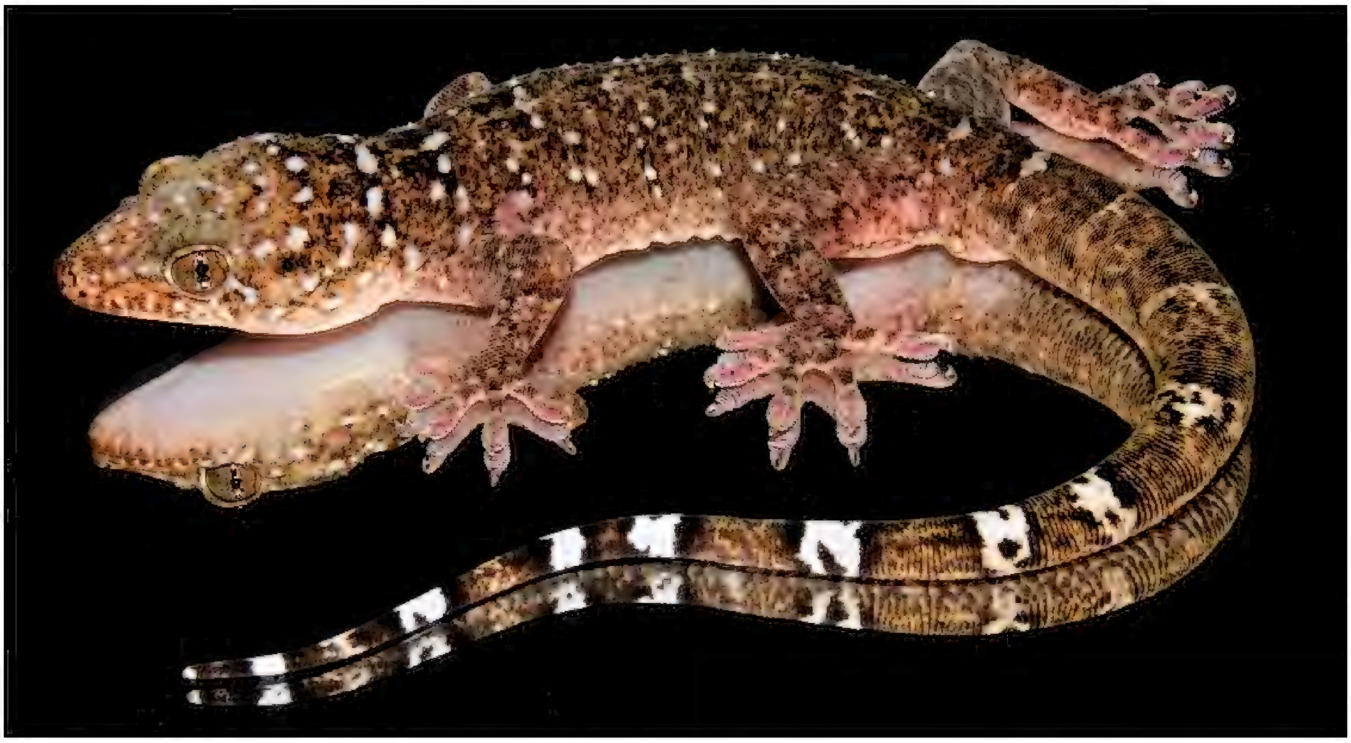

Figure 1. Adult male of *Gekko ernstkelleri* Rösler, Siler, Brown, Demegillo et Gaulke, 2006 (photo courtesy T. Hofmann).

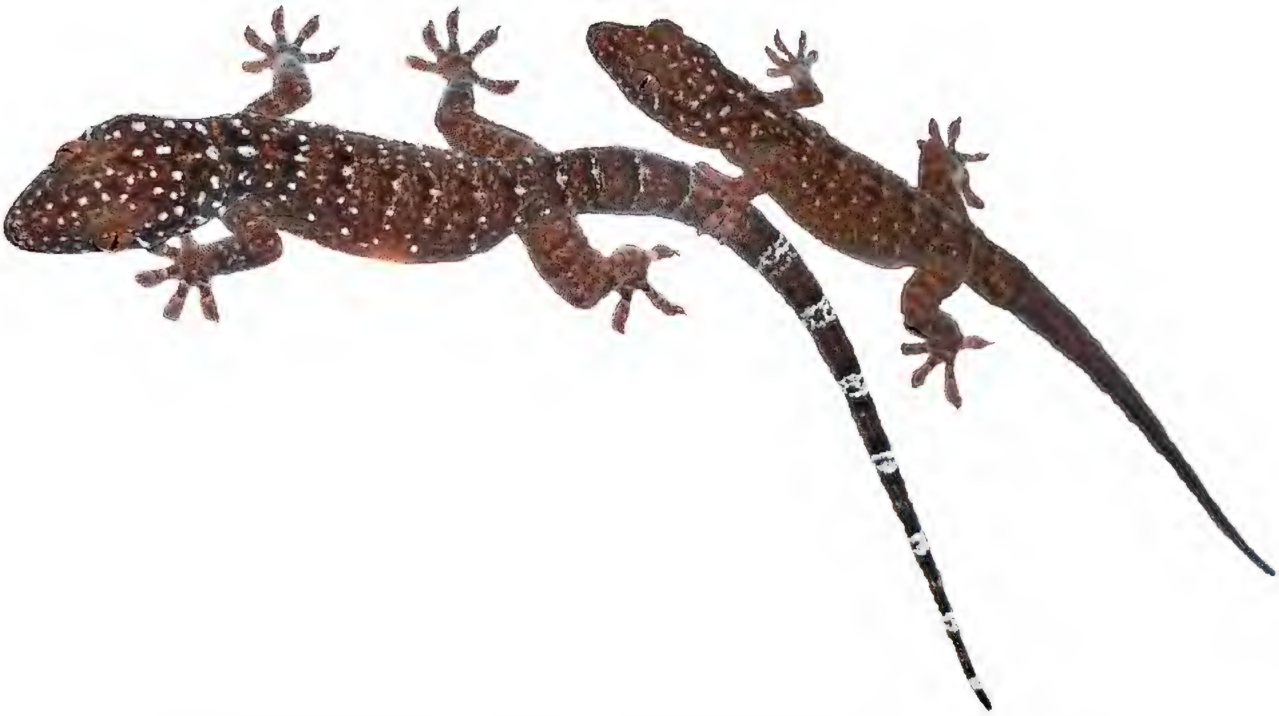

Figure 2. Adult couple of *Gekko ernstkelleri*, male on the left and female on the right. The female has an almost completely regenerated tail.

The diurnal and annual range of temperature and humidity in caves and deep limestone crevices is more consistent than the outside air temperature and humidity (Alcala & Alcala 2005), besides, karst habitats offer a wealth of places for egg-deposition.

Behaviour

Gekko ernstkelleri is a mainly nocturnal species. In nature, first active individuals were observed at around 4:30 pm, before darkness, but their main activity time starts during sunset,

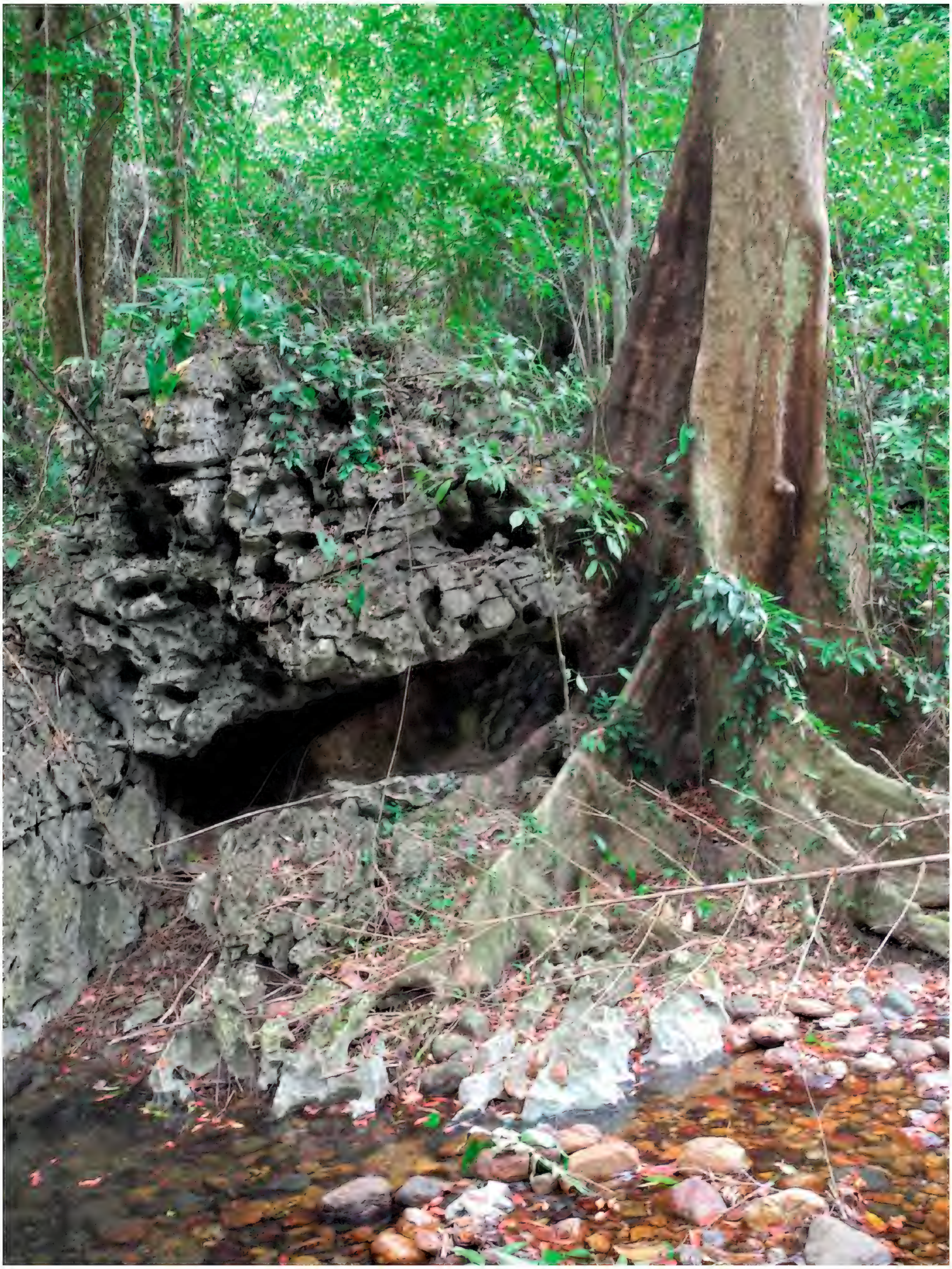

Figure 3. *Gekko ernstkelleri* often inhabits deeply karstified limestone walls and outcrops (NW Panay Peninsula).

between six and seven pm (Rösler *et al*., 2006; Gaulke 2011). In their terraria, active specimens were frequently observed outside their retreats during daytime, especially following cool winter-nights, to occupy sites close to light- and heat sources. Even intensive movements outside their terraria usually did not induce flight behaviour during their diurnal thermoregulation periods, while during almost complete darkness, the same optical stimuli (in a distance of 0.5 to 2 m from the terraria) led to flight behaviour. Acoustic stimuli without accompanying movements, such as human voices, usually did not induce flight behaviour.

The *G. ernstkelleri* were kept in pairs in their terraria throughout the investigation period of six years, however, the partners were exchanged a few times during this time. During this time, no intra-sexual aggressive behaviour was observed, and even an occasional exchange of the females did not lead to noteworthy problems.

It was not possible to keep *G. gigante*, another endemic gecko from the Philippines, for a long period of time under similar conditions as *G. ernstkelleri*. Even the first socialization of a mature male and a mature female of *G. gigante* (in March) resulted in fierce biting's. This aggressive behaviour was probably induced by a non-compatible hormonal state of the pair. The obviously sexually motivated male attacked the disinterested female of *G. gigante* fiercely, inflicting severe bite injuries on head and body, and biting off most toes of the female's hind limbs. Those conflicts can be interpreted as intraspecific territorial behaviour. Sexual unmotivated females of *G. gigante* provoke the same behaviour in males, as they would show towards conspecifics of the same sex. Continued aggressive behaviour of males towards sexual unmotivated females of *G. gigante* within artificial, limited habitats is known from other members of the genus *Gekko* as well (Kreuzer & Grossmann 2003).

At the start of the investigation period, threatening behaviour among captive males of *G. ernstkelleri* was regularly observed, because they had constant visual contact with each other (later, visual covers were provided). The threatening behaviour started with staring at each other, followed by wriggling movements of the slightly raised tails. A trial to socialize two males had to be cancelled. A direct confrontation involuntarily led to

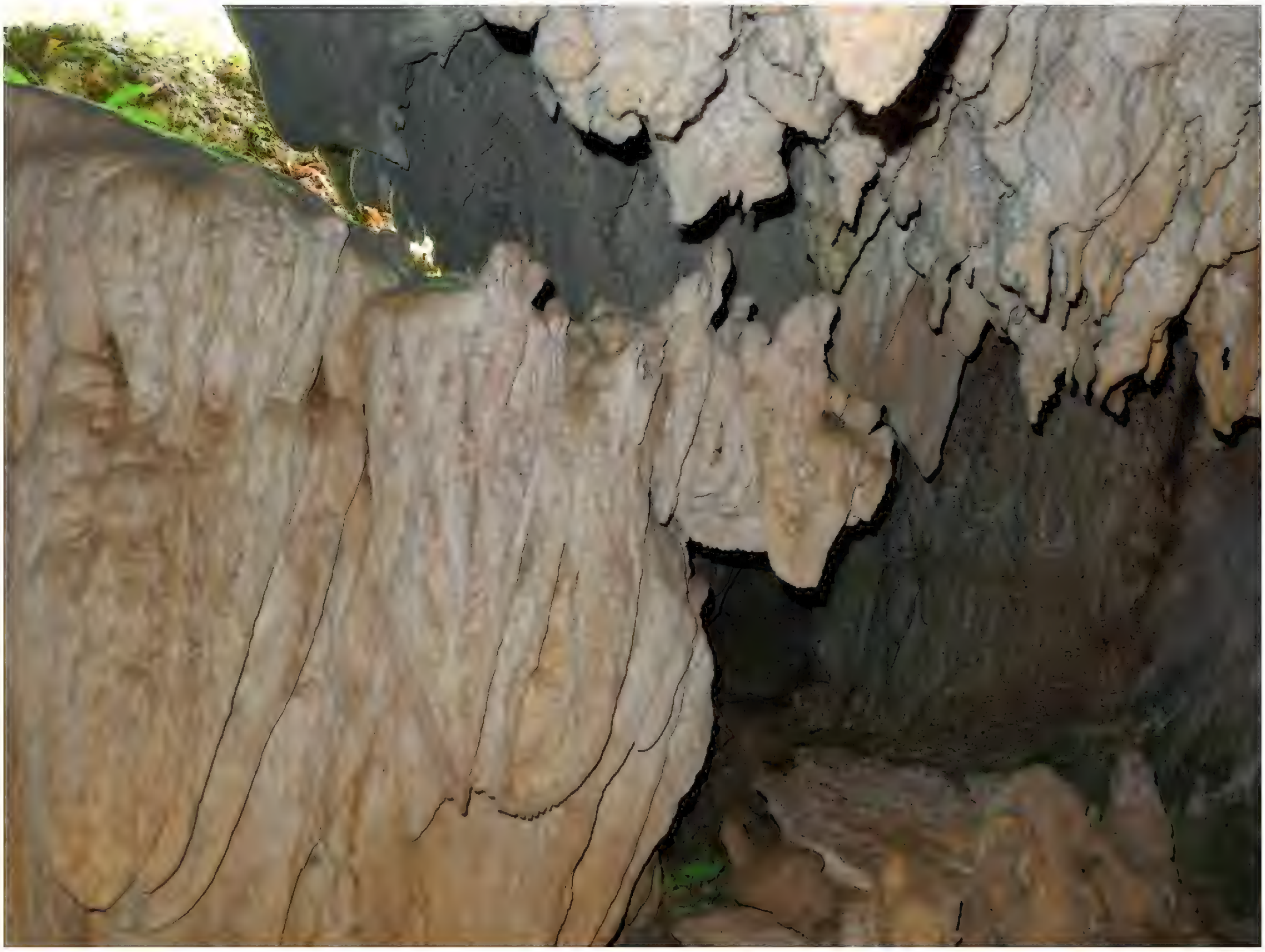

Figure 4. The entrance area of Sapsapon Cave, NW Panay Peninsula, inhabited by *Gekko ernstkelleri*.

the mentioned threatening behaviour, followed by fast biting attacks of the dominant individual (the resident of the respective terrarium). The attacked male tried to flee, but was chased and bitten by the dominant male until it was removed from the terrarium.

Unfortunately, the mating behaviour never could be observed in *G. ernstkelleri*. Typical external indications such as bite marks in the nuchal region of the female could never be detected. Mating calls of males, as known from different *Gekko*-species (Mertens 1946; Böhme *et al*. 1985; Tang *et al*. 2001; Jono & Inui 2012; Chen *et al*. 2016) could not be detected. *Gekko ernstkelleri* is not voiceless. The geckos can emit a slight fear scream or a defense call.

Many Squamata have developed species behavioural models for the protection of their offspring. Protective behaviour starts with the search for adequate egg-laying sites, but can also involve active defense of eggs and offspring (Deegener 1918; Somma 1990).

In the case of *G. ernstkelleri*, observations in natural habitats proved egg-guarding behaviour (according to Shine 1988). Egg-clutches (often attached to crevices on cave ceilings) usually are guarded by one or two adults, which attack intruders such as herpetologists, if getting close to the eggs. Even during daytime, when at the first moment no gecko can be seen, adults will immediately appear at the clutch site if they notice disturbances (Gaulke 2011; 2012).

Egg-guarding behaviour also occurred in the terraria. It could be directly observed if eggs were not attached inside hiding places (plastic tubes) but to open, easily accessible areas. Directly after egg-deposition, adults remained in the direct vicinity of the eggs. Sometimes, both partners were seen close to the eggs, but more frequently the female. Unlike observations in their natural habitat, the adults in the terraria took refuge in hiding places if disturbed, for example by handlings inside the terrarium, and did not try to defend their eggs. A while after egg-deposition, the females only sporadically visited their clutch-sites. A more or less constant egg-guarding behaviour was only observed, if the eggs were attached inside plastic tubes. Inside the tubes, almost always one or both adults were seen during controls throughout the entire incubation period. However, they were easily dispelled from their guarding-post, without showing any signs of threatening behaviour or trying to attack.

All behavioural modes in relation to eggs and hatchlings are summarized as “parental care” (Petzold 1984; Shine 1988). Within the geckos, three different stages of parental care can be clearly differentiated: precaution (search for, and eventually preparing of a suitable clutch-site), care (egg-guarding and egg-defence), and aftercare (defence of hatchlings). Only few gecko species show all three stages of parental care (Rösler 2005).

Stage one, searching for a suitable egg-deposition place, is strongly developed in *G. ernstkelleri*. In several caves with a high *G. ernstkelleri* population, even intensive searches did not reveal a single egg-clutch, obviously the eggs were hidden very carefully in deep crevices. On the other hand, sites considered as optimal by the geckos, were used for extended periods of time, often by several females. This was easily discernible

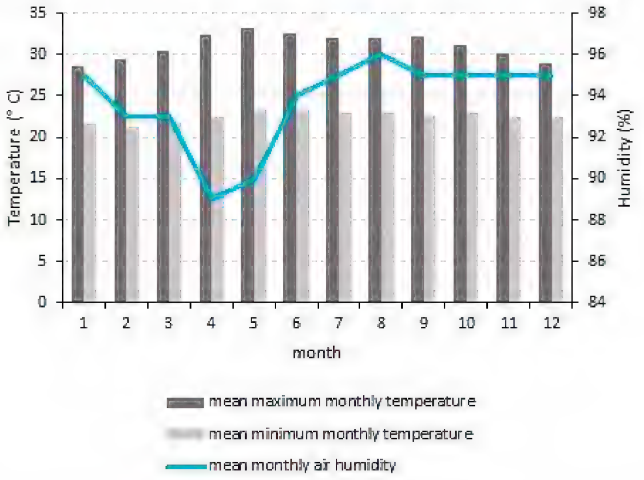

Diagram 1. Annual climate (1990-2005) of Capiz (N11°23.33, E122°37.67), Panay, the Philippines.
It should be noted that the microclimate within the cave habitats of *Gekko ernstkelleri* is more balanced and, in particular, the humidity is less subject to fluctuations.

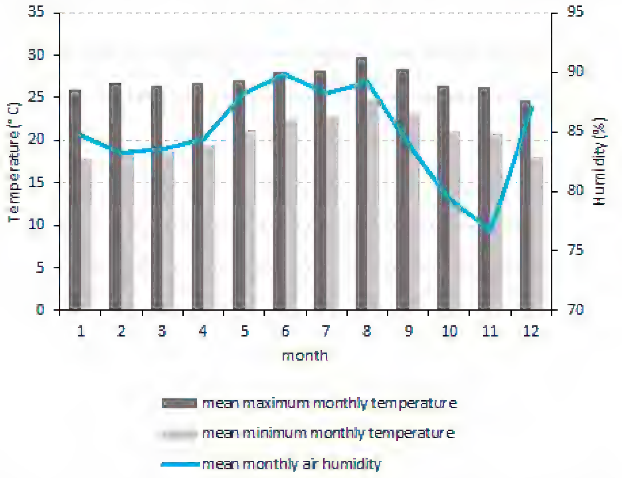

Diagram 2. Climatic conditions in the *Gekko ernstkelleri* terrariums in 2013 (deviations in the remaining years are almost non-existent).
The geckos were kept in cooler and drier conditions than within their habitat in Panay.

by egg-clutches of different developmental stages glued close to each other, often on the shell remains of already hatched eggs. As mentioned above, these places are regularly guarded by adults (Gaulke 2012).

Under natural conditions the parental care of *G. ernstkelleri* includes two of the three stages: precaution and care, while no indications of aftercare were observed. Observations under captive conditions revealed a somewhat different behaviour. In one case, the highly developed eggs were devoured by one parent (it is not known whether the male or the female, and it is not known whether the embryos were alive or deceased directly prior to the time of egg-eating). The devouring of empty eggshells is a normal part of the reproductive behaviour of females, this way they fill up their depleted calcium resources effectively. If the embryos were dead prior to the egg eating, the adult must have detected the condition olfactorily, and used the eggs as a natural resource. But if the embryos were still alive, it means that no bonding towards the own eggs existed during the time of egg eating. This would be a sign of a behavioural disorder.

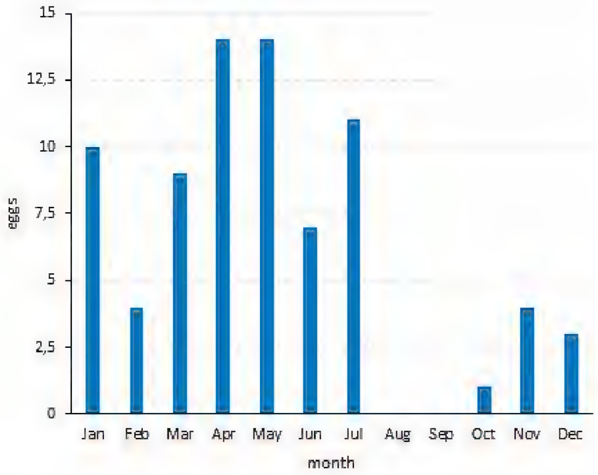

Diagram 3. Monthly egg production (total n = 77) in terrariums of four females of *Gekko ernstkelleri* from 2013-2019.

Two times, the own offspring (each time two hatchlings) was devoured by the parents, both times by different pairs. It is unknown, whether both parents or only one adult was involved in this cannibalistic behaviour. In both cases, the juveniles hatched during night-time from eggs glued inside plastic tubes, where they were guarded by the parents.

In several species of the genus *Gekko*, e.g. *G. gecko* (Linnaeus, 1758), *G. grossmanni* Günther, 1994, *G. petricolus* Taylor, 1962, *G. siamensis* Grossmann et Ulber, 1990, *G. smithii* Gray, 1842, and *G. vittatus* Houttuyn, 1782, observations in captivity revealed a complex parental care (Koch 1968; Grossmann & Mudrack 1987; Grossmann & Stein 1988; Treu 2001; Kreuzer & Grossmann 2003; Grossmann 2004). In other species, e.g. *G. badenii* Szczerbak & Nekrasova, 1994, the own hatchlings fall into the predator-prey system of the adults (Hofmann 2007). Cannibalism could also be observed in *G. monarchus* (Rösler 1981; 1982), a species related to *G. ernstkelleri*. As phyletic criterion for both species, a low-threshold of parental care could be primordial, or else, was newly acquired because of the discontinuation of predation pressure in the terrarium.

Among the Gekkonidae, parental care is highest developed within the genus *Gekko*. According to present knowledge the complexity of parental care gives no group-specific indications on infrasubgeneric level (Table 1). However, in many *Gekko* species parental care has not yet been investigated thoroughly. Further studies are necessary to ascertain which behavioural elements constitute parental care in other groups of affinity (respectively subgenera sensu Wood *et al*. 2020) within the genus *Gekko*, and whether a group-specific distinction will be indicated.

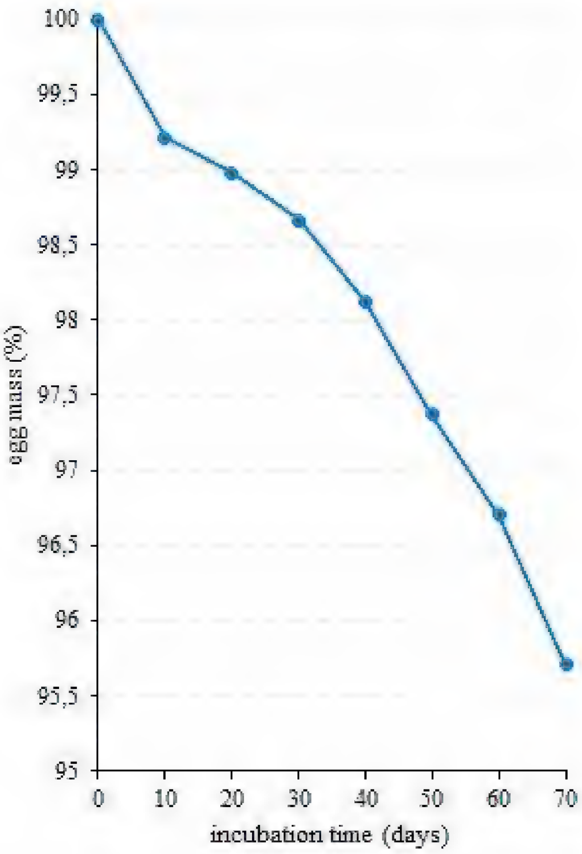

Diagram 4. Weight loss during the incubation period of an egg from *Gekko ernstkelleri*. The egg was hatched in an incubator, incubation temperature fluctuated between 25-32 °C, relative air humidity > 90 %.

Reproduction

Females used for breeding were photographed, to enable recognition based on individual colour patterns. They were numbered 1 to 4, and their SVL and BW determined in 2014 and 2018. In numerical sequence, mean values are: female 1 SVL 78 mm, BW 16.27 g, female 2 SVL 79 mm, BW 12.63 g, female 3 SVL 84 mm, BW 15.80 g, female 4 SVL 84 mm, BW 16.00 g.

All four female *G. ernstkelleri* were breeding, captive conditions for the four pairs (terrarium size, equipment, climatic conditions, diet) were identical. Females 1 and 4 deposited fertile eggs before completing their second year. Female 2 had reached an age of two years and three months before depositing its first fertile eggs, and female 3 four years and seven months. The late start of egg laying in female 3 is not necessarily due to a delay in reaching sexual maturity. Possible reasons might be an acyclic hormonal process of the sexual partners, individual sexual unacceptance, or physiological problems.

Table 1. Parental care of species from three related groups of the genus *Gekko*.
Legends: The taxonomic structures follow the concept of Wood *et al.* (2020). Data on *Gekko kuhli* (Stejneger, 1902) and *Gekko lionotum* (Annandale, 1905) from Grossmann (2008), for further information see text. The species-specific behavior of parental care is divided into three sections and assessed as non-existent (0) or existing (1).

Taxon	Provision	Care	Aftercare
Subgenus *Gekko*			
G. gecko	1	1	1
G. siamensis	1	1	1
G. smithii	1	1	1
Subgenus *Archipelagekko*			
G. ernstkelleri	1	1	0
G. monarchus	1	1	0
Subgenus *Lomatodactylus*			
G. badenii	1	1	0
G. grossmanni	1	1	1
G. petricolus	1	1	1
G. vittatus	1	1	1
Subgenus *Ptychozoon*			
G. kuhli	1	1	0
G. lionotum	1	1	0

Between July 5, 2013 and 10, 2019, the four females produced 44 egg-clutches all in all. Most clutches were deposited by females 1 (20) and 4 (14). Female 2 produced six clutches between 2015 and 2018, female 3 four clutches between 2016 and 2019. It could not be clarified, whether the strongly differing number of egg-clutches produced by the four females had physiological reasons or has to be seen in context with captive conditions (e.g. no free choice of mates).

On Panay, *G. ernstkelleri* lives in groups. Knowledge on intraspecific patterns of relations within these social structures does not exist. Individual relationships (empathy) may influence the egg-laying activities of a female as well as physiological circumstances.

The duration of the breeding season as well as the number of clutches within the breeding season of the kept *G. ernstkelleri* differed among the four individuals. The longest recorded breeding season lasted around nine and a half months (October 16, 2017 to July 27, 2018). Within this timespan, F_1 produced four egg-clutches in different time gaps. During another breeding season, F_1 deposited the same number of clutches within only about five months (November 20, 2015 to April 30, 2016). None of the females laid more than four egg-clutches within one egg-laying cycle.

Similarly, quantitative graduated frequencies are known from other gecko species. Osadnik (1987) for example observed an individually differing contribution to egg production in a group of eight female *Phelsuma dubia* (Boettger, 1881) throughout a two-year field study. Within six months, the females produced between one and nine clutches. The big difference in clutch quantity was partly age- and size dependent. Nevertheless, two same-sized females produced three versus nine clutches within an egg-laying season of six months. Differing egg-deposition frequencies influence the population dynamic. A regularly spaced egg-deposition frequency among all reproductive active females leads to an exponential population growth.

Of the 44 egg-clutches produced by the four females, 11 contained a single egg, and 33 two eggs each (mean clutch size 1.78±0.42). Eleven of the 77 eggs (14%) were infertile.

Clutches containing only one egg were produced throughout the breeding season, but much less so during the beginning and during the midst of the breeding season (9% and 18%, respectively). Most single-egg clutches were laid towards the end of the breeding season (73%), a strong indication for a state of exhaustion of the reproductive active females towards the end of the breeding season.

Different places for egg-deposition, partly consisting of natural materials, partly of artificial materials, were available in the respective terraria. These were vertical and sloping crevices between stone slabs (oil shale), large and flat pieces of different types of bark, and plastic tubes with a diameter of 35 mm and 50 mm, respectively.

The egg-laying behaviour of *G. ernstkelleri* is fixed genetically. Within its natural habitat, females glue their eggs in small crevices at cave walls or, more often, on the ceiling of a cave (Fig. 5). In the terraria fertile eggs were also glued to surfaces, whereby hard inorganic materials such as glass or hard plastic were preferred over organic matters such as oak bark or cork. Egg-clutches with two eggs were always glued in pairs together (Fig. 6). Infertile eggs were sometimes found on the ground, or as a smeared mass on the glass pane of the terraria. Horizontal surfaces (the terrarium floor), as well as unstructured clay soil or heaps of foliage are rather untypical egg-deposition sites. Only once a clutch was glued to a dry leaf on the ground (pers. com. T. Hofmann).

At the start, the females preferred the thinner plastic tubes (diameter 35 mm) for egg-deposition, while no clutches were found in the plastic tubes with a diameter of 50 mm.

To determine egg-weight, the preferred egg-laying sites were modified later on. Therefore, the interior of the plastic tubes was lined with thin paper. This was meant to enable the observer to remove the eggs from the surface after deposition easily. However, it turned out that this manipulation of the hitherto preferred egg-laying sites resulted in the females looking for alternative egg-deposition sites. Obviously they regarded paper as an unsuitable substrate to glue the eggs on. While choosing suitable sites for egg-deposition, *G. ernstkelleri*'s primary selective criterion is the quality of the substrate, while locality is of secondary importance. The preference of substrate quality over protecting shelters such as crevices means that it is considered of higher importance ethologically.

Searching for new egg-laying sites, the eggs were now glued to freely accessible, mostly moderately warm and darkish places along the lower part of the sides of the terrarium glass. The females did not use the available hiding places in crevices. Lighter positions at the upper part of the glass panes, which were exposed to more radiation heating, were rarely used. Part of the eggs glued outside the plastic tubes were protected by a transparent, air-permeable cover by the observer.

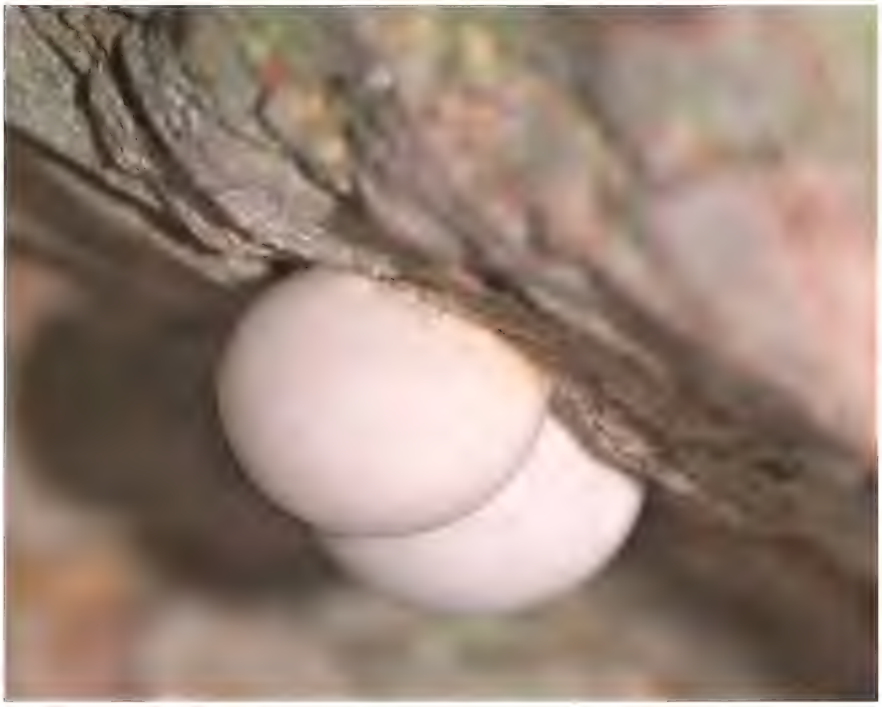

Figure 5. A clutch of *Gekko ernstkelleri* stuck to the cave ceiling in a natural habitat, the Philippines, Antique Province, Pandan Municipality, Barangay Sto. Rosario.

The complete natural reproductive cycle of *G. ernstkelleri* in nature is unknown. Developing eggs were observed from October to end of June, however, no field observations were conducted during the months of July to September. Most newly laid eggs were found in March. The tropical climate of its natural distribution makes it likely that they are reproducing throughout the year (compare tropical taxa in Fitch 1970).

The climatic conditions provided for *G. ernstkelleri* in captivity throughout the observation period differed from the climate within their natural habitat. Humidity as well as temperature provided for the geckos in their terraria was lower (Diagrams 1 & 2). It is known that geckos kept in captivity can tolerate differences in temperature and humidity up to a certain degree. In some species it could be determined already that these differences lead to more or less pronounced deviation from the natural species-specific reproductive cycle (Rösler 2005).

Within the terraria *G. ernstkelleri* laid eggs from October to July of the following year. During August and September, no egg-laying activities were noted (Diagram 3). It is noteworthy that part of the egg-laying activities occurred during the cool phase of husbandry. The observations show that females of *G. ernstkelleri* were able to carry eggs full term beside the decreasing, relatively low ambient temperatures starting in October. Actually a high number of egg-clutches were recorded in January 2015, 2016, and 2019. A total of 10 eggs were laid during these months. Only the relatively low day- and night temperatures of the two following months obviously influenced egg-development, resulting in a low number of eggs. In February the egg-production declined drastically to only four eggs, followed in March by a slight increase to seven eggs. In April and May egg-laying activities reached their peak (14 eggs each). During the winter months February/March neither a prolonged gestation period nor a resorption of eggs were observed (Rösler 2005).

To present knowledge, all members of the genus *Gekko* glue their eggs to a substrate (Okada *et al*. 2002; Rösler 2005; Kreuzer *et al*. 2013). In about two-thirds of the eggs of *G. ernstkelleri* they were glued more or less at one of the egg-poles lying in their longitudinal axis, in the rest either flat parallel, or slightly tilted towards the longitudinal axis. This has to be considered for the assessment of egg shape, and the computation of egg volume, respectively. In eggs, which were glued at a pole, the plane adhesive surface amounts to at least two-thirds of egg-width or egg-length, respectively, compared to being glued parallel to their longitudinal axis. In the first instance this results in an objective decrease of the egg-length, in the second case of the egg-width. Accordingly, data on the proportion EL/EW, as well as on the volume, must be regarded as approximate values.

Only 26% of all eggs could be measured, eggs glued to unfavourable sites could not be measured. They had a length of 14.85-18.85 mm (16.40±1.08, n=20), and a width of 11.40-13.90 mm (12.48±0.81, N = 20). Eggs laid in captivity differ much less in size than those laid in nature. The determined size of eggs laid in nature is: length 14.4-16.0 mm (N = 10) and width 10.9-12.8 mm (N = 10) (Gaulke 2012). These slight deviations have to be considered as normal intraspecific variations.

The form of the eggs of *G. ernstkelleri* is roundish to oval. The value EL/EW is 1.07-1.42 (1.31±0.07, N = 20). Comparing the value of both egg-axes, egg-length has a higher range (4 mm) and variation (*V* 1.15) than egg-width (2.5 mm, *V* 0.6). The higher variation determined in egg length is not a species specific character, as it is typical for most species of the Gekkota (Kratochvil & Frynta 2005).

Merely a single egg was glued to a plastic tube lined with paper, and therefore could be recovered. Its weight immediately following deposition was 1.3967 g. During the incubation period of 76 days, an egg mass decreased 10.5% (Diagram 4). A egg mass reduction during embryogenesis is typical for all hard-shelled eggs of the Sphaerodactylidae, Phyllodactylidae, and Gekkonidae (Rösler 2005). The determined egg mass reduction in the *G. ernstkelleri* egg does not differ significantly from those of other species in these three families (Rösler in prep.).

The incubation period of geckonid eggs shows species-specific differences. Besides, the embryonic development is influenced by the ambient temperature (Rösler 1998). The prevalent, relatively low temperatures measured at the egg-laying sites of *G. ernstkelleri* in the terraria resulted in a significantly prolonged incubation time. At the egg-laying sites with the lowest temperatures (10-15 cm above ground, distance towards the heat-source 25-30 cm), the day/night temperatures ranged between 22°C and 15.5°C during the winter months, and between 25.5°C and 17.5°C during the summer months. During the cool period, mean day temperatures taken directly at the egg-deposition sites ranged below 20°C (February, minimal daily mean 18.8°C). Under these conditions, the juveniles of *G. ernstkelleri* hatched after 82-179 days (117±24, n=33). Only two clutches were deposited close to the light source (fluorescent lamp), at a distance of six cm. The fluorescent lamp operated 12 hours daily. The temperature at the clutch site reached 29-33°C during daytime, and 19-26°C during nighttime. One of the clutches deposited close to the light source hatched after 64 days, the second one after 76 days.

Juveniles of *G. ernstkelleri* hatched during daytime as well as during the night (Fig. 7). If they hatched within the terraria, they were taken out on the day of hatching, and measured and weighed immediately. The SVL of newly hatched juveniles ranged from 29.5 to 39.5 mm (33.84±2.35, n=45), the TaL from 31.0 to 47.0 mm (40.43±3,52, n=45). The TaL/SVL ratio is 1.00-1.37 (1.20±0.06, n=45).

In some clutches embryos underwent normal development until reaching hatching time (egg teeth in upper jaw completely developed (Rösler 2001)), but still deceased in the egg. Eggs successfully hatching and those containing fully developed but dead embryos were exposed to the same incubation conditions. Therefore, reasons for the death of some of the embryos are unknown. A connection with the time of oviposition as well as obvious malformations of the embryos as reason for death can be excluded.

In part of the hatchlings, the TaL corresponded with the SVL or was just slightly longer. This was the case mainly in juveniles hatching too early. During embryonic development of *G. ernstkelleri*, as in all oviparous geckos, an early negative allometric tail growth occurs (Noro *et al*. 2009). After reaching a certain embryonic SVL state this relation reverses, resulting in a proportionate faster growth of the TaL. A balanced ratio between SVL and TaL during hatching is untypical for *G. ernstkelleri*. What causes a premature hatching of juveniles could not be determined. Characteristics for premature hatching were, beside of the untypical body proportions, remains of egg yolk within the egg shells, or egg yolk clinging to the umbilical cord of the hatchlings. No size differences between the juveniles hatched after fully completed embryonic development in the terraria, and those hatched in nature, were recorded. Recorded hatchling sizes within the type locality of *G. ernstkelleri* were: SVL 34.7-35.5 mm and TaL 40.7-41.4 mm (N = 4 (Gaulke 2012)). The smaller size range of the measurements compared to those of the hatchlings bred in captivity is a result of the lower number of individuals measured.

In the juveniles hatching with completely absorbed egg yolk, the SVL values 38-45% (41±3, N = 30) of the SVL of the mother. Similar proportions are known from *G. gigante* (42%), *G. palmatus* Boulenger, 1907 (40%), and *G. petricolus* (47%), while juveniles of the larger species *G. siamensis* (SVL of adult 136.5 mm) are comparatively smaller (35% of the maternal SVL).

The weight of juvenile *G. ernstkelleri* hatched in captivity with completely absorbed egg yolk is 0.8917-1.1632 g (0.9975±0.0764, N = 25), and in nature 0.90-1.04 g (Gaulke 2012). Usually, the juveniles hatched with completely absorbed yolk sack. Those having not yet completely absorbed the egg yolk, showed a significantly lower weight. Hatchlings with torn off, only partly absorbed, or yolk sack clinging to the umbilical cord weighed 0.6382-0.8018 g (0.7048±0.0553, N = 12). The survival capability of these juveniles was low.

The weight of fully developed juveniles of *G. ernstkelleri* amounts to 5.6-7.8% (6.3±0.6, N = 25) of the weight of the mother. Similar ratio data are displayed by the Philippine species *G. gigante* (6.0%), and *G. mindorensis* (4.9-5.2%), as well as by the Vietnamese species *G. palmatus* (5.2%).

After hatching, we attempted to retrieve the eggshells as completely as possible. Sometimes this was impossible because the females discovered the empty eggshells within short time, and devoured them. The saved eggshells were dried for one day by 60 °C, afterwards the thickness and weight of the shells were determined. The eggshells of *G. ernstkelleri* are 82-188 µm thick (136±28, n=32), which amounts to 0.44-0.99% (0.80±0.13, n=18) of the egg-length. Their weight is 0.1646-0.2552 g (0.2009±0.0247, n=18). This is equivalent to about 15.8% of the weight of freshly deposited eggs (n=1).

The reproductive effort conducted by a female for the production of an egg-clutch, based on the calculation of relative clutch mass (RCM), depends mainly on clutch size. The energy expense to produce a clutch with only one egg compared to the normal sized clutch containing two eggs is about half only. For the calculation of the relative clutch mass two formulas were used:

$$\mathrm{RCM} = \mathrm{cv}/\mathrm{fbw} \times 100\ [\%]$$

(cv = clutch volume, fbw = female body weight, after Pianka & Pianka (1976))

$$\mathrm{RCM} = \mathrm{fwcm}/(\mathrm{fwcm}+\mathrm{fbw}) \times 100\ [\%]$$

(fwcm = fresh wet clutch mass, fbw = female body weight, after Hielen (1993))

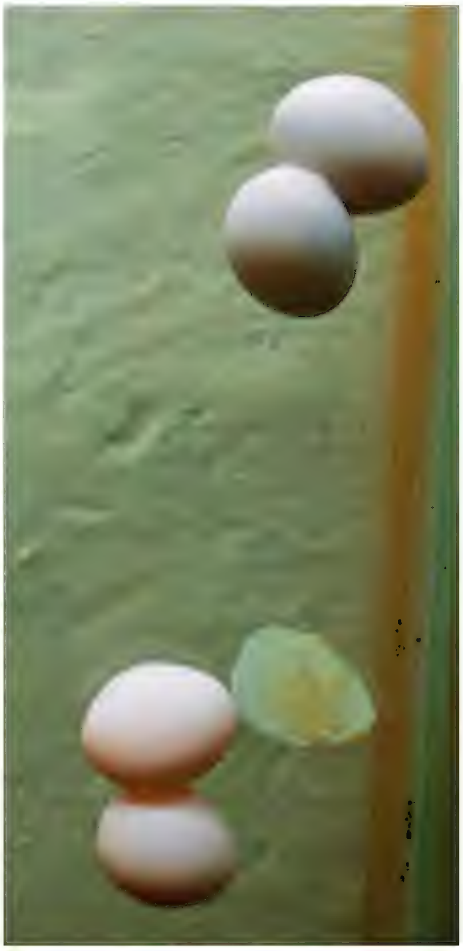

Figure 6. Two clutches of *Gekko ernstkelleri* glued on a glass panel. The upper clutch is older than the lower one. To the right of the lower clutch is an egg mark of a previously placed single egg.

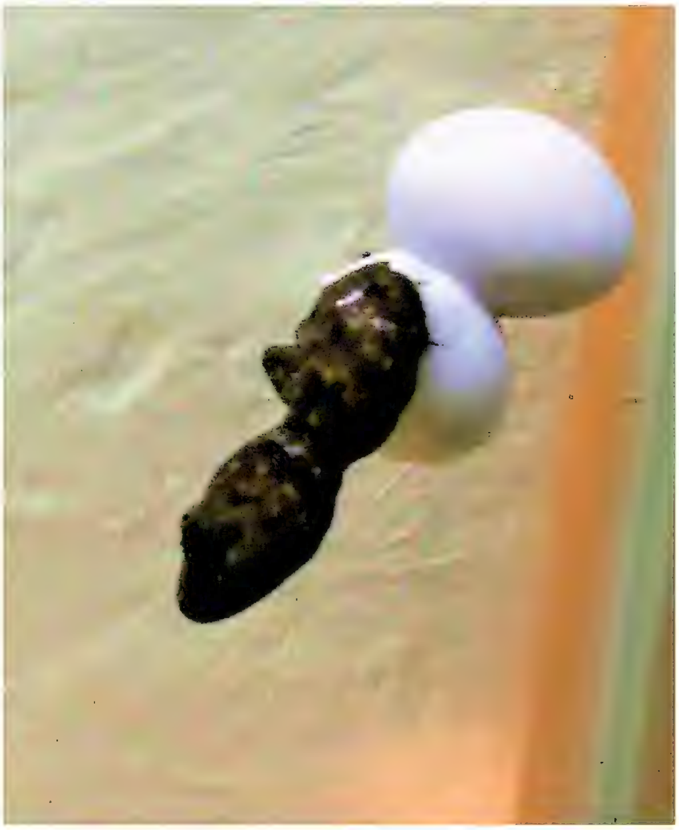

Figure 7. Hatching of *Gekko ernstkelleri* in the terrarium

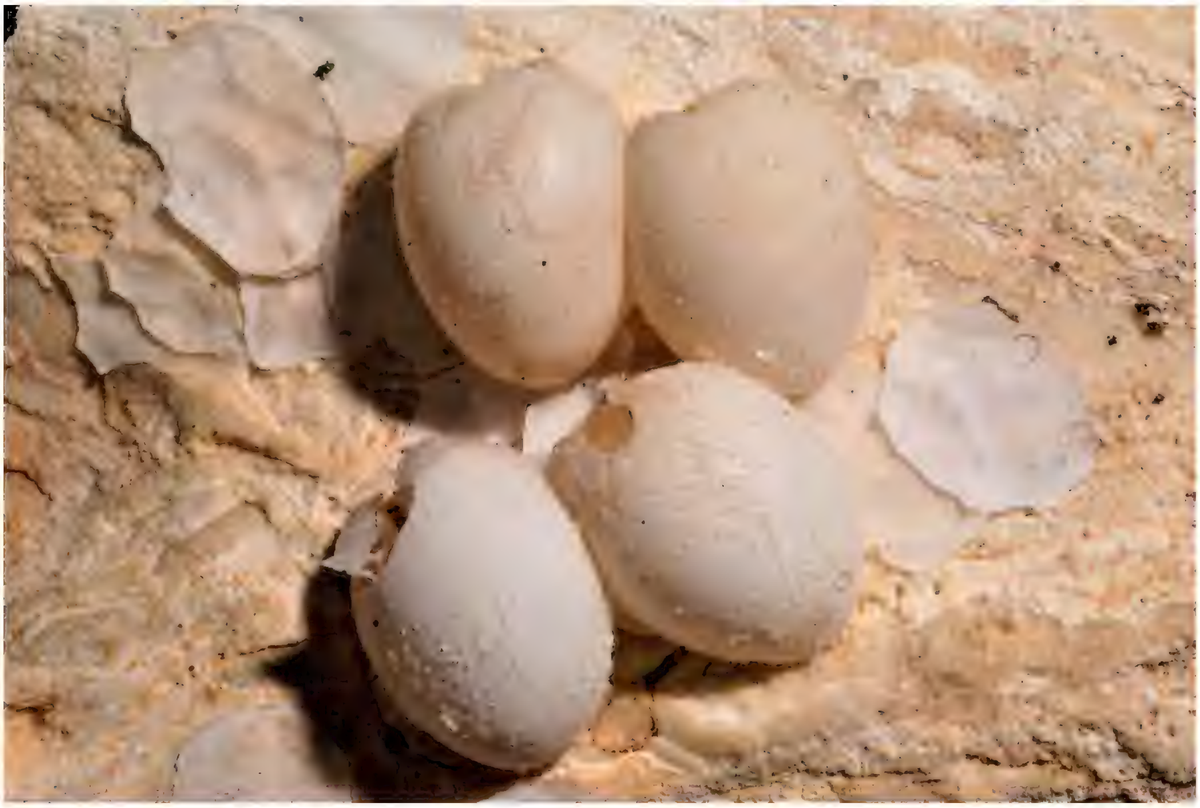

Figure 8. Nibble traces on the newly hatched eggs from *Gekko ernstkelleri*. Eggshells are valuable calcium resources and are regularly eaten by the females.

One quarter of the *G. ernstkelleri* egg-clutches contained one egg. Those eggs had a slightly bigger volume (1.30-1.61 cm^3, mean 1.41±0.17, n=3) compared to those from clutches containing two eggs (1.03-1.87 cm^3, mean 1.32±0.25, n=17). Possibly, a female invests more from her own limited body resources in the production of a single egg. However, statistics do not support this hypothesis, since differences in egg-volume between both samples were insignificant (Mann-Whitney U Test, p 0.8181). However, only few single-egg clutches (n=3) were available.

Results regarding the reproductive effort of *G. ernstkelleri* are presented in Table 2.

Calculated using the formula by Pianka & Pianka (1976), *G. ernstkelleri* spends less effort in egg production (RCM for two eggs 19.95%, one egg 10.20%) than *G. gigante* (RCM of two eggs 28.33%, one egg 12.15%), but more than *G. monarchus* (RCM of two eggs 13.50%, one egg 5.90%).

Table 2. Relative clutch mass of *Gekko ernstkelleri*.

Cluch size	**Mean**	**sd**	**min/max**	**n**	**Formula according to**
two eggs	19.95	1.67	18.03-21.08	3	Pianka & Pianka (1976)
one egg	10.20	0.48	9.87-10.54	2	Pianka & Pianka (1976)
one egg	9.34			1	Hielen (1993)

Conclusions

This paper gives comprehensive data on the reproductive biology of an endemic Philippine gecko species, resulting from extensive investigations and observation in captivity during a time span of several years, supplemented by field investigations. Analytical comparisons with other species of the genus *Gekko*, as well as with other squamates of the herpetofauna of Panay are planned.

Acknowledgements

We are grateful to Thomas Hofmann (Zittau, Germany) for an animated exchange of information, and the contribution of photos. Maren Gaulke highly appreciates the support of the Department of Environment and Natural Resources and the Protected Areas and Wildlife Bureau (DENR and PAWB, respectively, Quezon City, the Philippines), given to the projects conducted by her as member of the Philippine Endemic Species Conservation Project (PESC). We thank Olivier S. G. Pauwels (Royal Belgian Institute of Natural Sciences, Brussels) for reviewing the manuscript and providing instructive information.

References

Alcala E. L., Alcala A. C. 2005. Aspects of ecology and threats to the habitats of three endemic herpetofaunal species on Negros and the Gigantes Islands, Philippines. – *Silliman Journal* **46**, No 2: 169–194.

Böhme W., Hutterer R., Bings W. 1985. Die Stimme der Lacertidae, speziell der Kanareneidechsen (Reptilia: Sauria). – *Bonner Zoologische Beiträge* **36**, No 3/4: 337–354.

Brown R. M., Oliveros C. H., Siler C. D., Diesmos A. C. 2008. A new gecko from Babuyan Islands, northern Philippines. – *Herpetologica* **64**, No 3: 305–320.

Brown R. M., Oliveros C. H, Siler C. D., Diesmos A. C. 2009. Phylogeny of *Gekko* from the northern Philippines, and description of a new species from Calayan Island. – *Journal of Herpetology* **43**, No 4: 620–635.

Brown R. M., Siler C. D., Oliveros C. H., Diesmos A. C., Alcala A. C. 2011. A new *Gekko* from Sibuyan Island, Central Philippines. – *Herpetologica* **67**, No 4: 460–476.

Brown W. C., Alcala A. C. 1962. A new lizard of the genus *Gekko* from the Philippine Islands. – *Proceedings of the Biological Society of Washington* **75**: 67–70.

Brown W. C., Alcala A. C. 1978. Philippine lizards of the family Gekkonidae. – *Silliman University Natural Science Monograph Series* **1**: 1–146.

Chen J, Jono T., Cui J., Yue X., Tang Y. 2016. The acoustic properties of low intensity vocalizations match hearing sensitivity in the webbed-toed gecko, *Gekko subpalmatus*. – *Plos ONE*,: 1–12 doi:10.1371

Deegener P. 1918. *Die Formen der Vergesellschaftung im Tierreiche*. Verlag von Veit & Comp, Leipzig: 420 pp.

Ferner J. W., Brown R. M., Sison R. V., Kennedy R. S. 2001. The amphibians and reptiles of Panay Island, Philippines. – *Asiatic Herpetological Research* **9**: 34–70.

Fitch H. S. 1970. Reproductive cycles of lizards and snakes. – *The University of Kansas Museum of Natural History Miscellaneous Publication* **52**: 1–247.

Gaulke M. 2011. *The herpetofauna of Panay Island, Philippines*. Chimaira, Frankfurt am Main: 390 pp.

Gaulke M. 2012. Höhlengeckos. – *Aquaristik Fachmagazin* **44**, No 6: 82–88.

Grossmann W. 2004. *Gekko smithii* Gray, 1842. – *Sauria* **26**, No 3, Supplement: 627–634.

Grossmann W. 2008. *Faltengeckos Ptychozoon kuhli & Ptychozoon lionotum*. Natur und Tier – Verlag, Münster: 63 pp.

Grossmann W., Mudrack W. 1987. Beitrag zur Haltung und Nachzucht von *Gekko smithii* (Gray, 1842). – *Sauria* **9**, No 3: 25–30.

Grossmann W. & Stein, V. 1988. *Gekko petricolus* Taylor, 1962 – Haltung und Zucht im Terrarium. – *Sauria* **10**, No 3: 27–30.

Hielen B. 1993. Unterschiedliche Fortpflanzungsstrategien bei Geckos der Gattung *Tarentola*, Gray, 1825. – *Salamandra* **28**, No 3/4: 179–194.

Hofmann T. 2007. *Der Vietnam-Goldgecko*. Vivaria Verlag, Meckenheim: 63 pp.

Jono T., Inui Y. 2012. Secret calls from under the eaves: acoustic behaviour of the Japanese house gecko, *Gekko japonicus*. – *Copeia* **2012**, No 1: 145–149.

Koch H. 1968. 3 Jahre Tokehzucht. – *Aquarien Terrarien* **15**, No. 2: 67.

Kratochvil L., Frynta D. 2005. Egg shape and size allometry in geckos (Squamata: Gekkota), lizards with contrasting eggshell structure: why lay spherical eggs? – *Journal of Zoological Systematics and Evolutionary Research* **44**: 217–222.

Kreuzer M., Grossmann W. 2003. Beobachtungen an *Gekko ulikovskii* Darevski & Orlow, 1994 und *Gekko grossmanni* Günther, 1994 im Terrarium. – *Sauria* **25**, No 3: 3–11.

Kreuzer M., Grossmann W., Hofmann T. 2013. Terrarienbeobachtungen an *Gekko badenii* (Sauria: Gekkonidae). – *Sauria* **35**, No 3: 41–47.

Linkem C. W., Siler C. D. Diesmos A. C., Sy E., Brown R. M. 2010. A new species of *Gekko* (Squamata: Gekkonidae) from central Luzon Island, Philippines. – *Zootaxa* **2396**: 37–49.

Mertens R. 1946. Die Warn- und Drohreaktionen der Reptilien. – *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **471**: 1–108.

Noro M., Uejima A., Abe G., Manabe M., Tamura K. 2009. Normal developmental stages of the Madagascar ground gecko *Paroedura pictus* with special reference to limb morphogenesis. – *Developmental Dynamics* **238**: 100–109.

Okada S., Izawa M., Ota H. 2002. Growth and reproduction of *Gekko hokouensis* (Reptilia: Squamata) on Okinawajima Island of the Ryukyu Archipelago, Japan. – *Journal of Herpetology* **36**, No 3: 473–479.

Osadnik G. 1987. Untersuchungen zur Reproduktionsbiologie des madagassischen Taggeckos *Phelsuma dubia* (Boettger, 1881). PhD thesis, Universität Bochum, 311 pp. [unpublished]

Petzold H.-G. 1984. Aufgaben und Probleme bei der Erforschung der Lebensäußerungen der Niederen Amnioten. – *Milu* **5**, No 4/5: 485–786.

Pianka E. R., Pianka H. D. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australia desert. – *Copeia* **1976**, No 1: 125–142.

Rösler H. 1981. Ohne Besonderheiten? – *Gekko monarchus* (D. & B. 1836). – *Sauria* **3**, No 2: 7–11.

Rösler H. 1982. Nachtrag zu meinem Artikel „Ohne Besonderheiten – *Gekko monarchus* (D. & B. 1836)“ (Sauria 2/81). – *Sauria* **4**, No 2: 23–24.

Rösler H. 1998. Bemerkungen zur Fortpflanzungsbiologie von Geckonen – Aufzeichnungen aus den Jahren 1993 bis 1996 (Sauria: Gekkonidae). – *Gekkota* **1**: 64–175.

Rösler H. 2001. Die Eizähne einiger Geckos (Sauria: Gekkota). – *Gekkota* **3**: 99–124.

Rösler H. 2005. *Vermehrung von Geckos*. Verlag Elke Köhler, Offenbach: 270 pp.

Rösler H., Bauer A. M., Heinicke M. P., Greenbaum E., Jackman T., Nguyen T. Q., Ziegler T. 2011. Phylogeny, taxonomy, and zoogeography of the genus *Gekko* Laurenti, 1768 with the revalidation of *G. reevesii* Gray, 1831 (Sauria: Gekkonidae). – *Zootaxa* **2989**: 1–50.

Rösler H., Siler C. D., Brown R. M., Demegillo A. D., Gaulke M. 2006. *Gekko ernstkelleri* sp. n. – a new gekkonid lizard from Panay Island, Philippines. – *Salamandra* **42**, No 4: 197–211.

Shine R. 1988. Parental care in reptiles: 275–330. *In:* Gans C., Huey R. B. (eds) *Biology of Reptilia*. Volume 16. Ecology B, Defense and life history. Alan R. Liss Inc., New York: 659 pp.

Somma L. A. 1990. A categorization and bibliographic survey of parental behaviour in lepidosaurian reptiles. – *Smithsonian Herpetological Information Service* **81**: 1–53.

Tang Y., Zhuang L., Wang Z. 2001. Advertisement calls and their relation to reproductive cycles in *Gekko gecko* (Reptilia, Lacertilia). – *Copeia* **2001**, No 1: 248–253.

Treu B. 2001. Haltung und Zucht des Streifengeckos, *Gekko vittatus* Houttuyn, 1782. – *Sauria* **23**, No 4: 31–35.

Wood P. L., Guoa X., Travers S. L., Su Y. C., Olson K. V., Bauer A. M., Grismer L. L., Siler C. D., Moyle R. G., Andersen M. J., Brown R. M. 2020. Parachute geckos free fall into synonymy: *Gekko* phylogeny, and a new subgeneric classification, inferred from thousands of ultraconserved elements. – *Molecular Phylogenetics and Evolution* **146**: 1–11.

Received: 23.ii.2020.
Accepted: 25.ix.2020.